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Community ecology

Shoreline urbanization interrupts allochthonous subsidies to a benthic consumer over a gradient of lake size

Eric R. Larson[1,*], **Julian D. Olden**[1] **and Nisikawa Usio**[2]

[1]*School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98195-5020, USA*
[2]*Center for Transdisciplinary Research, Niigata University, Niigata 950-2181, Japan*
**Author for correspondence* (*lars9570@uw.edu*).

The role of resource subsidies across ecosystem boundaries has emerged as an important concept in contemporary ecology. For lake ecosystems, this has led to interest in quantifying the contribution of terrestrial allochthonous carbon to aquatic secondary production. An inverse relationship between habitat area and the role of allochthonous subsidies has been documented on marine islands and assumed for lakes, yet there have been no tests of this pattern among benthic (lake bottom) consumers. Here, we used carbon stable isotopes to trace terrestrial allochthonous and benthic autochthonous carbon use by the crayfish *Pacifastacus leniusculus* over a gradient of lake area, productivity and urbanization. Consistent with findings from terrestrial islands, habitat size dictated the importance of allochthonous subsidies, as *P. leniusculus* transitioned from using predominantly terrestrial carbon in small lakes to an increased reliance on autochthonous production in larger lakes. However, shoreline urbanization interacted with this pattern, particularly for small lakes where greater urbanization resulted in reduced use of allochthonous resources. As such, we provide, to our knowledge, the first confirmation of the predicted relationship between habitat size and importance of allochthonous subsidies to lake benthic consumers, but found that urbanization can interfere with this pattern.

Keywords: crayfish; lakes; resource subsidy; stable isotopes; urbanization

1. INTRODUCTION

The historical tendency by ecologists to consider adjacent aquatic and terrestrial ecosystems as isolated and non-interacting was overturned in recent decades through studies demonstrating the prevalence of resource subsidies between such habitats [1–3]. In lake ecosystems, this has led to debates on the contribution of terrestrial allochthonous subsidies to secondary production relative to autochthonous primary production [4,5]. These studies have prioritized the pelagic (open water) zone, while de-emphasizing the benthic (lake bottom) zone despite repeated calls to dedicate more research to benthic processes and organisms [6,7]. Investigations of allochthonous and autochthonous dynamics in benthic consumers of lakes are scarce and often limited to single-site case studies [8,9], failing to generalize trends over the large gradients of lake size and productivity that have enlightened pelagic food web work [10,11].

Reviews of carbon dynamics and spatial subsidies in lakes have assumed the diminishing importance of allochthonous subsidies with increasing habitat (lake) area [6,12]. This inverse relationship between habitat area (or perimeter : area) and the role of allochthonous subsidies has been famously documented on marine islands [1] and applied to flowing waters with the River Continuum Concept [13], which predicts that the considerable role of terrestrial resources in small headwaters should decrease with distance downstream and increasing river size. However, we are unaware of any formal test for this phenomenon among benthic habitats and consumers in the freshwater analogue of an island : the lake.

In this study, we used carbon stable isotopes to investigate the contribution of allochthonous and autochthonous resources to a benthic omnivore over a large gradient of lake size from a field study and literature review. We also evaluated lake productivity as a competing or potentially complementary mechanism in explaining patterns of allochthonous dependence, and considered the influence of shoreline urbanization on resource use. Urban development on lakes reduces riparian (near shore) vegetation and has been reported to interfere with allochthonous subsidies to the diets of lake consumers [14]. Our analysis provides, to our knowledge, the first empirical test of the major determinants influencing patterns of allochthony and autochthony in a benthic consumer with respect to lake size, productivity and urbanization, and highlights the importance of incorporating benthic consumers and processes in studies of lake food webs.

2. MATERIAL AND METHODS

The ratio of carbon isotope ^{13}C to ^{12}C ($\delta^{13}C$) provides a tracer of energy source origins because it is fixed by primary producers at photosynthesis and is conserved up food chains. In lake ecosystems, $\delta^{13}C$ is often used to discriminate between consumer use of pelagic (depleted in $\delta^{13}C$) and littoral (near shore) benthic resources (enriched in $\delta^{13}C$), with terrestrial allochthonous $\delta^{13}C$ being intermediate [10,15]. We used the signal crayfish *Pacifastacus leniusculus* as an integrator of benthic food web dynamics. Native to western North America but globally introduced, *P. leniusculus* is long-lived, wide-ranging, omnivorous and has been found to make minimal use of pelagic resources in previous studies [16]. Our analysis was dependent on $\delta^{13}C$ differentiation between terrestrial allochthonous and littoral benthic autochthonous resources while assuming minimal contribution of $\delta^{13}C$-depleted pelagic resources to our benthic consumer.

We collected *P. leniusculus* and allocthonous (terrestrial detritus) and benthic autochthonous (periphyton and macrophyte) resources from the littoral zone of 14 lakes in Washington State, USA and Hokkaido, Japan during the summers of 2008 and 2009. Tissue samples were dried at 60°C for 24 h, homogenized by mortar and pestle and 1 mg of *P. leniusculus* or 2–3 mg of plant matter was sent to the UC-Davis Stable Isotope Laboratory for analysis on a PDZ Europa 20–20 isotope ratio mass spectrometer. We also used recent *P. leniusculus* $\delta^{13}C$ values from a literature review for four additional lakes in western North America. *Pacifastacus leniusculus* sample sizes ranged from 6 to 20 per lake. Secchi disk depth (m), a standard limnological approach to measuring water transparency, was used as an estimate of lake productivity. We estimated the

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extent of urbanization by counting structures on lake shorelines from recent aerial photographs (structures km^{-1}). Lake attributes and literature sources are summarized in the electronic supplementary material. Lake area (log), urbanization (log + 1) and Secchi depth (inverse) were transformed for analysis.

A Welch *t*-test for separate variances was used to assess differences in allochthonous and benthic autochthonous $\delta^{13}C$. Linear regression and a test of homogeneity of slopes (ANCOVA) was applied to evaluate consistency in $\delta^{13}C$ values for these resources and *P. leniusculus* over the gradient of lake area. Multiple linear models of lake area, productivity and urbanization were developed to explain *P. leniusculus* $\delta^{13}C$. Model comparisons were performed with maximum-likelihood values from the linear models using the modified Akaike's Information Criterion (AICc) for small sample sizes, a model selection technique based on the trade-off between model accuracy and parsimony [17]. The relative likelihood that a model is the best given the dataset and candidate models was determined by comparing AICc values of individual models to the best performing model (δAICc) with differences <2 considered equivalent. Model comparisons were also performed using the proportional contribution of allochthonous resources to *P. leniusculus*, calculated from a stable isotope mixing model [18], in place of $\delta^{13}C$ (see the electronic supplementary material).

3. RESULTS

Allochthonous resources were significantly depleted in $\delta^{13}C$ relative to benthic autochthonous resources in the 14 study lakes we sampled ($t_{2,26} = -14.912$, $p < 0.001$). There was a positive but not significant trend of autochthonous $\delta^{13}C$ becoming more enriched with increasing lake area (slope = 1.398, $r^2 = 0.168$, $p = 0.145$; figure 1). Linear models incorporating lake area, urbanization and their interaction were the most supported for describing patterns of $\delta^{13}C$ in *P. leniusculus* (table 1). Particularly prominent was the strong relationship between lake area and enrichment of *P. leniusculus* $\delta^{13}C$ (slope = 3.360, $r^2 = 0.786$, $p < 0.001$; figure 1). The slope of *P. leniusculus* $\delta^{13}C$ enrichment with lake area was significantly steeper than that for benthic producers ($\text{ANCOVA}_{1,1,33} = 55.120$, $p < 0.001$). Urbanization exerted little influence on *P. leniusculus* $\delta^{13}C$ in large lakes ($\geq 10\ km^2$), but *P. leniusculus* was more enriched in $\delta^{13}C$ and presumably less supported by allochthonous subsidies in small lakes ($< 10\ km^2$) with a greater degree of urban development (figure 2). Productivity did not contribute to any of the most supported models of *P. leniusculus* $\delta^{13}C$ (table 1). Our results did not differ if proportional allochthonous contribution to *P. leniusculus* was analysed in place of $\delta^{13}C$ (electronic supplementary material).

4. DISCUSSION

Our study confirmed the previously untested prediction that lake area determines the importance of terrestrial allochthonous subsidies to benthic consumers, as $\delta^{13}C$ values for the crayfish *P. leniusculus* became enriched towards autochthonous resources and away from allochthonous resources with increasing lake area. We detected little effect of lake productivity on *P. leniusculus* $\delta^{13}C$ values. Urbanization did influence *P. leniusculus* $\delta^{13}C$ both directly and in an interaction with lake area. Interestingly, there was less apparent effect of urbanization in large lakes, where autochthonous resources consistently dominated *P. leniusculus* $\delta^{13}C$ values. By contrast, increasing

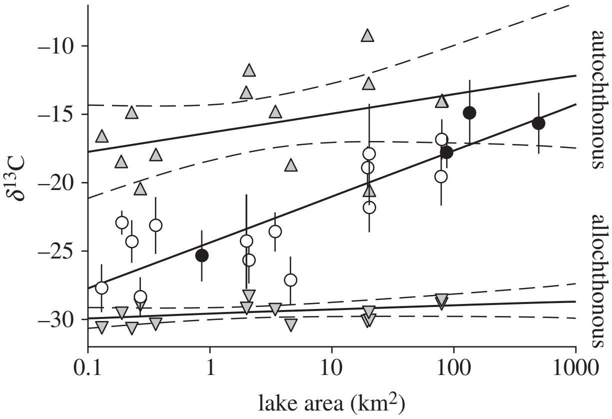

Figure 1. Mean $\delta^{13}C$ signatures of terrestrial allochthonous (down triangles) and benthic autochthonous (up triangles) resources over a gradient of lake size with mean (±s.d.) $\delta^{13}C$ for the benthic omnivore *Pacifastacus leniusculus* from lakes sampled during the summers of 2008 and 2009 (open circles) and literature values (closed circles). The regression formula for *P. leniusculus* is $y = -24.36 + 3.36x$ with an r^2 of 0.786.

shoreline urbanization in small lakes resulted in *P. leniusculus* $\delta^{13}C$ being enriched relative to predictions from lake area alone, indicating reduced availability of terrestrial subsidies to *P. leniusculus* in these systems.

Other studies have observed a similar pattern of $\delta^{13}C$ enrichment in pelagic producers and consumers with increasing lake area, attributed to either a diminished role for $\delta^{13}C$-depleted allochthonous carbon or increased prevalence of highly $\delta^{13}C$-enriched atmospheric carbon [10,11]. We found a weak positive relationship between $\delta^{13}C$ of littoral benthic producers and lake area, but this pattern did not influence the interpretation of our results when accounted for by using a stable isotope mixing model to calculate proportional allochthonous resource use in *P. leniusculus*. Although there is well-documented spatial and temporal variability of $\delta^{13}C$ values in aquatic producers [19], we argue that the enrichment of *P. leniusculus* away from consistent $\delta^{13}C$ values of allochthonous resources demonstrates diminished importance of terrestrial subsides with lake size and urbanization.

The effect of urbanization on $\delta^{13}C$ values in *P. leniusculus* is consistent with recent work documenting reduced terrestrial subsidies to lake consumers with shoreline development [14]. Detrital resources are important in stabilizing populations, communities and food webs, and the depressed availability of such terrestrial subsidies in highly urbanized small lakes may contribute to management problems from the conservation of populations to declining ecosystem services [20]. Our results also emphasize the potential role of benthic consumers in contributing to research on autochthonous and allochthonous support of lake secondary production [4,5]. For example, crayfish are ecosystem engineers in small streams owing, in part, to their tremendous capacity to process terrestrial detritus [21], and this function may be similarly important but overlooked in lakes. Benthic foraging fishes link

Table 1. The top five candidate models of *Pacifastacus leniusculus* δ^{13}C with AICc, δAICc, Akaike weights (w_i) and relative likelihoods.

model	AICc	δAICc	w_i	relative likelihood
area × urbanization	80.113	0	0.619	1.000
area + urbanization	81.784	1.671	0.268	0.434
area + urbanization + productivity	85.057	4.944	0.052	0.084
area	85.284	5.171	0.047	0.075
area + productivity	88.197	8.084	0.011	0.018

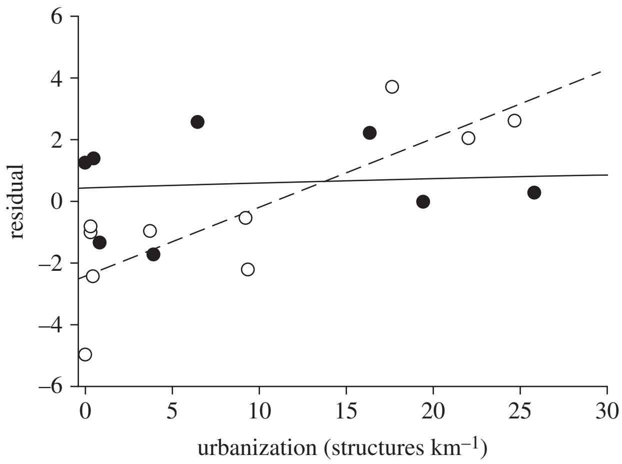

Figure 2. Residuals from *P. leniusculus* δ^{13}C regressed on lake area (figure 1) by the extent of shoreline urbanization for large ($\geq$10 km^2, closed circles, $y = 0.44 + 0.01x$, $r^2 < 0.01$) and small lakes ($<$10 km^2, open circles, $y = -2.41 + 0.22x$, $r^2 = 0.67$).

littoral production to pelagic habitats (i.e. following excretion of benthic-derived nutrients in the water column [7]), and consequently it seems likely that omnivorous benthic consumers like *P. leniusculus* may have a similar capacity to link terrestrial carbon to open water habitats through predatory fishes. We believe that the capacity for benthic omnivores to trace ecotonal coupling [22] should be incorporated into current debates on lake carbon dynamics, especially in the context of attributes like habitat size, productivity and urbanization.

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